Phylogeography of black bears (Ursus americaus) of the Pacific Northwest

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Abstract: Phylogeographic study across codistributed taxa provides temporal and spatial perspectives on the assemblage of communities. A repeated pattern of intraspecific diversification within several taxa of the Pacific Northwest has been documented, and we contribute additional information to this growing data set. We analyzed variation in two mitochondrial genes (cytochrome *b* and control region) for the black bear (*Ursus americanus*) and expand previous analyses of phylogeographic variation. Two lineages (coastal and continental) exist; the coastal lineage extends along the Pacific coast from the Takhin River north of Glacier Bay National Park, southeast Alaska, to northern California, whereas the continental lineage is more widespread, occurring from central Alaska to the east coast. Both lineages occur along the coast of southeast Alaska, where interlineage divergence ranged from 3.1 to 3.6% (uncorrected *p* distances). Multiple lineages of other species have also been identified from southeast Alaska, indicating a complex history for the assembly of biotic communities along the North Pacific coast. The overlapping of the distributions of the black bear lineages with those of other birds and mammals suggests comparable routes of colonization.

Résumé : L'étude phylogéographique de taxons qui cohabitent donne un aperçu temporel et spatial des associations qui définissent les communautés. Un pattern répété de diversification interspécifique chez plusieurs taxons des états du Pacifique nord-ouest constitue une information de base et nous ajoutons ici des détails supplémentaires sur cette base de données toujours croissante. Nous avons analysé la variation de deux gènes mitochondriaux (cytochrome *b* et région de contrôle) chez l'Ours noir (*Ursus americanus*) et nous ajoutons des données aux analyses préalables de la variation phylogéographique. Il existe deux lignées (côtière et continentale); la lignée côtière est répartie le long de la côte du Pacifique de la rivière Takhin, au nord du parc national de Glacier Bay, du sud de l'Alaska au nord de la Californie; la lignée continentale est plus dispersée, et sa répartition va du centre de l'Alaska à la côte est. Les deux lignées cohabitent le long de la côte du sud-est de l'Alaska et la divergence entre elles est de 3,1 à 3,6 % (*p* non corrigé). Des lignées multiples d'autres espèces existent aussi dans le sud-est de l'Alaska, ce qui reflète l'historique complexe des associations à la base des communautés biotiques de la côte du Pacifique nord. La répartition des lignées d'Ours noirs chevauche celle de certains oiseaux et de mammifères et ce chevauchement semble indiquer l'existence de voies de colonisation semblables.

[Traduit par la Rédaction]

Introduction

Communities are the products of present-day interactions (e.g., competition) operating within geographical and evolutionary frameworks that have developed through time (Ricklefs and Schluter 1993). Molecular phylogeography identifies the geographic distributions of lineages and, when examined across codistributed species, can provide a temporal and spatial perspective on the development of communities (Avise 1994, 1998). Phylogeographic study of a growing list of taxa distributed throughout North America suggests a repeated pattern of intraspecific diversification in the Pacific Northwest (e.g., mammals, Talbot and Shields 1996*a*; birds, Gill et al. 1993; amphibians, Green et al. 1996; plants, Soltis et al. 1997). If carefully documented, this pattern may provide insight into the history of community assembly in the region.

The black bear (*Ursus americanus*) shares this pattern of diversification. Two distinct lineages (coastal and continental) have been identified in northwestern North America (Cronin et al. 1991; Paetkau and Strobeck 1996; Byun et al. 1997; Wooding and Ward 1997). Byun et al. (1997, 1999) focus on Haida Gwaii (Queen Charlotte Islands), Vancouver Island, and mainland British Columbia and conclude that the "limited" distribution of the coastal lineage lends additional support for a purported Pleistocene glacial refugium on or near Haida Gwaii (but see Demboski et al. 1999). In contrast, Wooding and Ward (1997) conclude that the two major clades of black bears were historically separated into eastern and western forest refugia in southern North America. Through expanded sampling, we focus on a large region of potential sympatry at the northern and western distributional limits of the black bear. Our study also ties together previous analyses of black bears that were based on two different mitochondrial genes (Byun et al. 1997; Wooding and Ward 1997).

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Table 1. Sequences and associated references for primers used to amplify the mitochondrial cytochrome *b* gene and the control region.

Primer	Sequence (5′ to 3′)	Reference
MVZ4	GCAGCCCCTCAGAATGATATTTGTCCTC	Smith and Patton 1993
MVZ5	CGAAGCTTGATATGAAAAACCATCGTTG	Smith and Patton 1993
MVZ14	GGTCTTCATCTYHGGYTTACAAGAC	Smith and Patton 1993
MVZ23	TACTCTTCCTCCACGAAACJGGNTC	Smith and Patton 1993
MVZ16	AAATAGGAARTATCAYTCTGGTTTRAT	Smith and Patton 1993
Sorex37	TAYATRTTYYTAGATACATGAA	Demboski et al. 1999
L15774	GTAAAACGACGGCCAGTACATGAATTGGAGGACAACCAGT	Shields and Kocher 1991
TDKD	CCTGAAGTAGGAACCAGATG	Kocher et al. 1993

Materials and methods

DNA was extracted and amplified, using PCR (polymerase chain reaction), from frozen tissues (heart, kidney, liver, or skeletal muscle) of black bears from the Alaska Frozen Tissue Collection of the University of Alaska Museum (AFTC). Methods for extracting, amplifying, and sequencing DNA and for aligning sequences were carried out according to Lessa and Cook (1998), unless otherwise noted. Amplification reaction mixtures (50 μL) contained 1.5 mM $MgCl_2$, 0.02 mM of each dNTP, 1.0 μM of each primer, 1.25 U Perkin–Elmer AmpliTaq DNA polymerase, Perkin–Elmer 10× PCR buffer, and 1–100 ng whole genomic DNA. The mitochondrial (mt) markers, cytochrome *b* (cyt *b*) and control region, were amplified using a Perkin–Elmer GeneAmp PCR System 2400 under the following PCR conditions: 1 cycle of 94°C for 45 s, followed by 35 cycles of denaturation at 94°C for 10 s, annealing at 45°C for 15 s, and an extension at 72°C for 45 s, followed by 1 cycle of 72°C for 3 min. The primer pairs MVZ4 and MVZ5, MVZ14 and MVZ23, and MVZ16 and Sorex37 were used to amplify cyt *b* and the primer pair L15774 and TDKD was used to amplify the control region (Table 1). Both forward and reverse strands were sequenced for each individual.

A total of 74 black bears were examined. To synthesize previous studies based on different genes, we assessed sequence variation in both cyt *b* and the control region. Complete cyt *b* sequences (1140 base pairs (bp)) were generated from 14 samples; the control region was sequenced for four of these samples and restriction fragment length polymorphism (RFLP) profiles were determined for an additional 60 individuals (Table 2). Cyt *b* sequences were compared among eight black bears from southeast Alaska (three mainland and five island samples), two from the south-central region of Alaska, one from interior Alaska, and three from Oregon (Table 2). We added partial sequences (719 bp) of black bears from Haida Gwaii, Vancouver Island, mainland British Columbia, Yukon Territory, Alberta, and Washington (Byun et al. 1997). The Asiatic black bear (*Ursus thibetanus*) was used as an outgroup (1140 bp; Talbot and Shields 1996*b*). Identical sequences were removed, resulting in a reduced data set with 11 unique black bear sequences. All DNA sequences were deposited in GenBank under the accession number AF268258–268271.

Relationships among black bear cyt *b* sequences were examined using PAUP* (phylogenetic analysis using parsimony, version 4.0b3a; Swofford 1999). Phylogenetic trees were constructed using maximum parsimony with a branch-and-bound search. Character-state optimization was carried out with accelerated transformation, and an initial upper bound was computed via stepwise addition. Equal weights were applied to all characters. A strict-consensus tree generated from the equally parsimonious trees was subjected to 1000 bootstrap replications (using branch-and-bound).

We used RFLP analysis to screen additional individuals and document the geographic extent of these lineages in Alaska. Although this method did not reveal variation within each clade, existing sequences (cyt *b*, this study and Byun et al. 1997; mt control region, Wooding and Ward 1997) suggest that little intralineage variation exists in these mtDNA sequences. A restriction enzyme (*Alu*I) that differentially digested PCR products from each lineage was determined using DNA Strider 1.2 (written by C. Marck, Service de biochimie et du genetique moleculaire, 91191 Gif-sur-Yvette CEDEX, France). A portion of the cyt *b* (MVZ16–Sorex37) gene was amplified from four black bears of known mt lineages (two bears from each lineage; Table 2). A mixture of 9.0 μL PCR product, 1.0 μL New England Biolabs 10× buffer 2, and 0.2 μL *Alu*I restriction enzyme (2 U) was placed in a 37°C incubator for 2–3 h. DNA fragments were visualized on a 1.5% agarose gel stained with ethidium bromide. After RFLP banding patterns were established for the divergent lineages, we screened an additional 60 black bears to determine lineage profiles (Table 2).

Results

Base composition (A = 28.5%, C = 30.0%, G = 14.6%, and T = 26.9%) for cyt *b* was consistent with that of other mammals (e.g., Irwin et al. 1991; Talbot and Shields 1996*a*). Thirty-nine nucleotide sites differed between the two lineages (7 first-position, 3 second-position, and 29 third-position changes). Thirty-eight of these mutations were transitions. The single transversion (third position) did not result in an amino acid change; however, eight of the transitions (5 first-position and all 3 second-position changes) coded for different amino acids. Seven of the eight amino acid differences corresponded to hypervariable residues identified in a cyt *b* model (Irwin et al. 1991). A linear relationship (R^2 = 0.999) between third-position transitions and uncorrected *p* distances suggested that saturation has not been attained (Lara et al. 1996). These results were expected for PCR amplifications of genuine mt cyt *b* (as opposed to a nuclear pseudogene).

Parsimony analysis found 440 equally parsimonious trees (owing to short terminal branches) of 127 steps in length using 39 informative characters. All trees displayed two clades, corresponding to the coastal and continental lineages (Fig. 1). Divergence between lineages ranged from 3.1 to 3.6% (uncorrected *p*), whereas intra-lineage divergence was <0.5%.

We sequenced both cyt *b* and the control region for four individuals, to identify these genes for the two lineages. Alignment of our control-region sequences with those of Wooding and Ward (1997) verified that the two lineages they identified on the basis of control-region sequence were comparable to lineages identified by cyt *b* sequence (this study; Byun et al. 1997). RFLP analysis revealed 36 samples of the coastal lineage and 24 of the continental lineage (Table 2).

Table 2. Collection locations, lineage profiles, molecular methods used, and voucher numbers for specimens of *U. americanus*.

Locality	Lineage	Method(s)[a]	AFTC No(s).
Kupreanof Island, southeast Alaska	Coastal	Cyt *b*	18535
Mitkof Island, southeast Alaska	Coastal	R	22647, 22893
Castle Island, southeast Alaska	Coastal	Cyt *b*	18536
Prince of Wales Island, southeast Alaska	Coastal	Cyt *b*	12974, 14078
Prince of Wales Island, southeast Alaska	Coastal	R	12975, 14077, 21095, 24087, 24088, 24098, 24885, 24890, 24892, 24897, 24898, 24975, 24979, 24980
Revillagigedo Island, southeast Alaska	Coastal	Cyt *b*, ctrl, R	20101
Revillagigedo Island, southeast Alaska	Coastal	R	20102, 24086, 24090, 24092, 24093, 24094, 24886, 24887, 24889, 24891, 24893, 24971, 24972, 24982
Takhin River, southeast Alaska	Coastal	R	28214
Helm Bay, southeast Alaska	Coastal	R	24097, 24099
Bull Head Cove, southeast Alaska	Coastal	R	24888
Boca de Quadra, southeast Alaska	Coastal	R	24100
Nakat Inlet, southeast Alaska	Coastal	Cyt *b*	24096
Cascade Range, northern Oreg.	Coastal	Cyt *b*, ctrl, R	
Cascade Range, northern Oreg.	Coastal	R	21118
Coast Range, central Oreg.	Coastal	Cyt *b*	21119
Cascade Range, southern Oreg.	Coastal	Cyt *b*	21120
Beaver Quadrangle, Alaska	Continental	R	12973
Big Delta Quadrangle, Alaska	Continental	R	2397
Circle Quadrangle, Alaska	Continental	R	14394
Fairbanks Quadrangle, Alaska	Continental	R	10001
Kenai Quadrangle, Alaska	Continental	R	3633
Kenai Quadrangle, Alaska	Continental	R	3634
southeastward Quadrangle, Alaska	Continental	Cyt *b*	22954
Talkeetna Quadrangle, Alaska	Continental	Cyt *b*	16110
Tanana Quadrangle, Alaska	Continental	R	1252
Wisoutheastman Quadrangle, Alaska	Continental	Cyt *b*, ctrl, R	895
Juneau, southeast Alaska	Continental	R	14578, 28217
Juneau, southeast Alaska	Continental	Cyt *b*, ctrl, R	14581
Taku Harbor, southeast Alaska	Continental	R	28215
Stephen's Passage, southeast Alaska	Continental	R	28216
Holkam Bay, southeast Alaska	Continental	R	14579
Windham Bay, southeast Alaska	Continental	Cyt *b*	14582
Windham Bay, southeast Alaska	Continental	R	14583
Yukon Territory, Canada	Continental	R	27083, 27084, 27085, 27086, 27087, 27088, 27089, 27090, 27091, 27092
Cascade Range, central Oreg.	Continental	R	21121

Note: Quadrangles from United States Geological Service quadrangle maps (1 : 250 000) are given for south-central and interior Alaska samples.
[a]Automated sequencing of the mitochondrial cytochrome *b* gene (cyt *b*) or the mitochondrial control region (ctrl), or screening with a restriction-enzyme digestion (R).

Discussion

Several mammals are represented by divergent lineages in the Pacific Northwest, including black bears (this study; Byun et al. 1997; Wooding and Ward 1997), brown bears (*Ursus arctos*; Talbot and Shields 1996*a*), dusky shrews (*Sorex monticolus*), and marten (*Martes americana*; Demboski et al. 1999). All these lineages converge in southeast Alaska; however, it is unclear whether they were derived from a shared historical event (e.g., see Avise 1998; Bermingham and Moritz 1998). The coastal lineage of black bears minimally extends from the Takhin River north of Glacier Bay National Park, southeast Alaska (this study), south to northern California (Wooding and Ward 1997). The widespread continental lineage extends from interior Alaska south to Oregon and New Mexico and eastward to Newfoundland and Florida (Fig. 2; this study; Cronin et al. 1991; Paetkau and Strobeck 1996; Byun et al. 1997; Wooding and Ward 1997).

Contact between the two lineages may exist in Oregon, Montana, British Columbia, Alberta, and southeast Alaska (this study, Cronin et al. 1991; Byun et al. 1997; Wooding and Ward 1997). These regions should be characterized further using nuclear markers, to assess potential nuclear introgression. For example, Paetkau et al. (1998) demonstrated male-mediated gene flow between two mt lineages of brown bears in southeast Alaska using microsatellite markers.

The phylogeographic patterns for brown and black bears have been attributed to two general hypotheses: (1) coastal

Fig. 1. One of 440 equally parsimonious trees generated from cytochrome *b* gene sequences (this study; Talbot and Shields 1996*b*; Byun et al. 1997) of black bears (*U. americanus*) with a branch-and-bound search. Individuals with identical sequences are included in the tree. Branch lengths are shown above bars, and bootstrap values generated from the strict-consensus tree (out of 1000 replicas) are shown below bars. Samples in boldface type were sequenced for this study. Sequences for all other samples (Talbot and Shields 1996*b*; Byun et al. 1997) were downloaded from GenBank (accession numbers in parentheses).

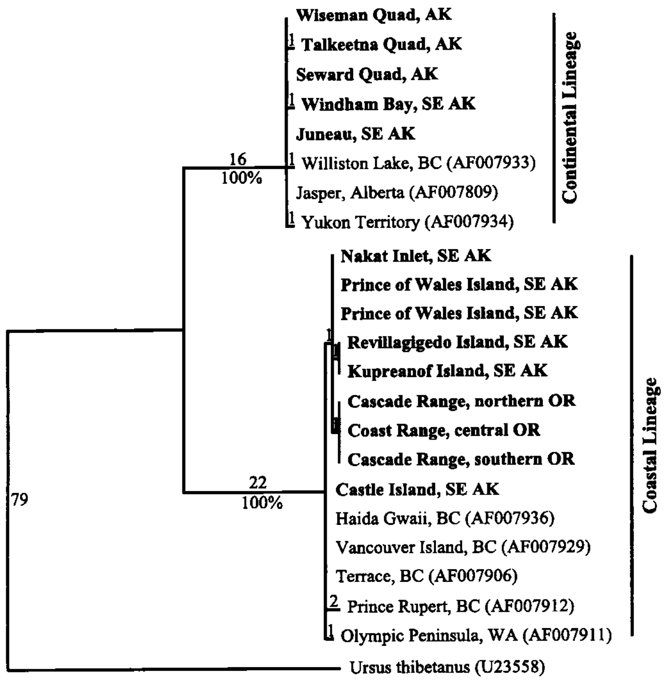
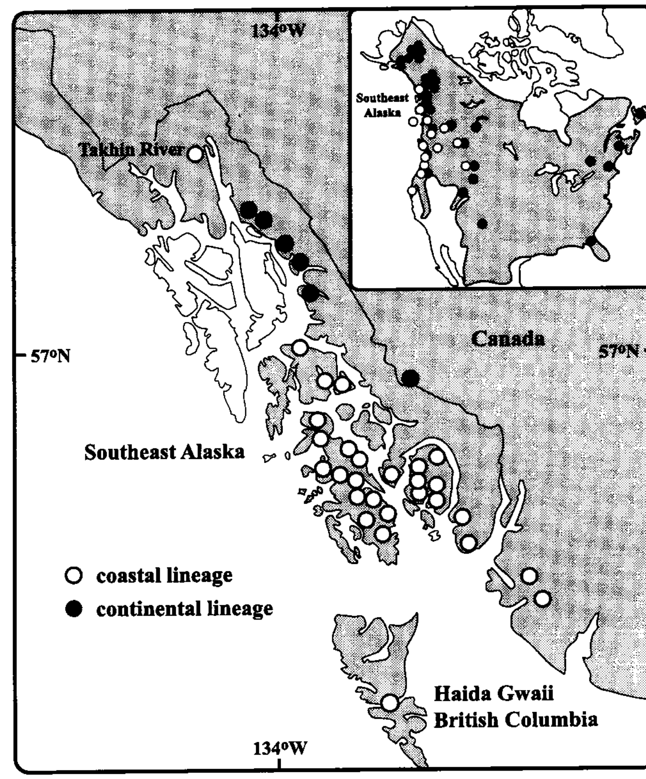


Fig. 2. Sample localities for black bears (*U. americanus*) from southeast Alaska (this study) and Canada (Byun et al. 1997). Open and closed circles represent black bear samples belonging to the coastal and continental mitochondrial lineages, respectively. Shaded areas denote the distribution of black bears modified from Hall (1981). The inset map plots sample localities from all studies (this study; Cronin et al. 1991; Byun et al. 1997; Wooding and Ward 1997).

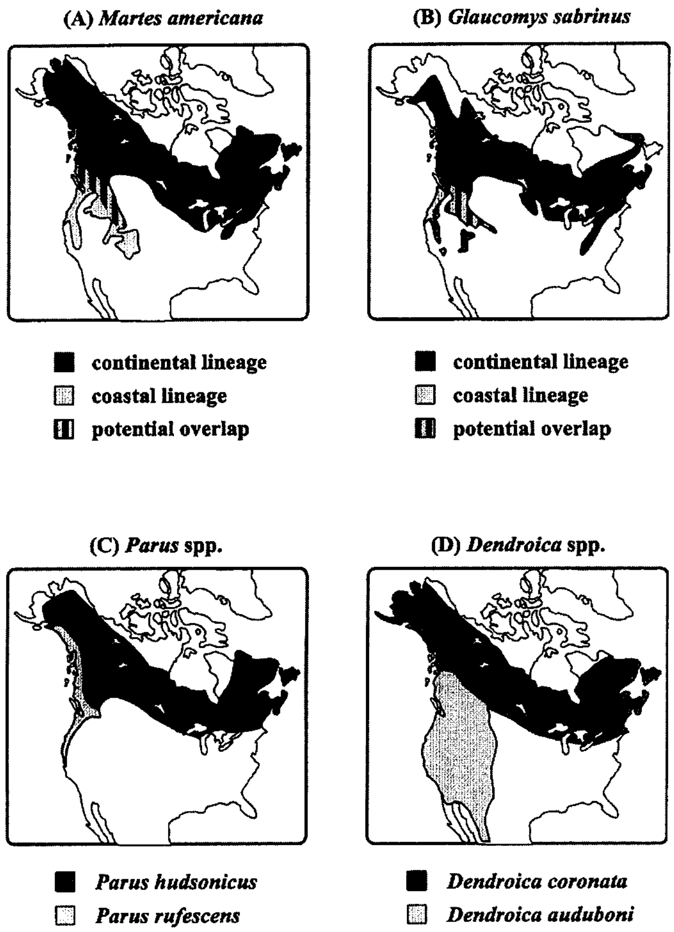


lineages were isolated in a northern coastal refugium (or refugia), such as Haida Gwaii, British Columbia, or southeast Alaska, while continental lineages were isolated in a southern refugium (or refugia) located south of the Pleistocene ice sheets in western and (or) eastern North America (Heaton et al. 1996; Byun et al. 1997) or (2) both lineages were isolated in separate southern refugia (Wooding and Ward 1997). Our results extend the known geographic range of the coastal lineage of black bears northward (into southeast Alaska). They also confirm that the western "clade B" (which extends into northern California) of Wooding and Ward (1997) identified by the control region is the same as the coastal lineage of Byun et al. (1997) identified by cyt *b*. Therefore, the coastal lineage of black bears is not "restricted to Haida Gwaii, Vancouver Island, and coastal regions of mainland British Columbia" (Byun et al. 1997, p. 1651).

Compelling evidence exists suggesting that an ice-free refugium was present in Hecate Strait (east of Haida Gwaii; named the Haida Gwaii glacial refugium) during a portion of the past glaciation (see Barrie et al. 1993; Byun et al. 1999). Crucial fossil evidence dating to the glacial maximum (27 500 – 16 000 BP) has not been revealed (Heusser 1989), therefore attempts to infer that the refugium supported black bear populations (Byun et al. 1997) remain speculative, particularly given the wide geographic extent of the coastal lineage (California to Alaska). Extensive geographic sampling, which includes independent loci, should be combined with other analytical methods, to explore the location of source populations for these lineages and, therefore, the presumed locations of refugia (Rogers and Harpending 1992; Rogers 1995; Templeton et al. 1995; Templeton 1998).

Delineating phylogeographic patterns of codistributed flora and fauna may provide a view of whether the expansion and contraction of habitats and their associated fauna were synchronous during glacial and interglacial cycles in western North America. Graham et al. (1996, pp. 1601 and 1605) conclude that "species that make up mammal communities in the contiguous United States have responded to late Quaternary environmental fluctuations in a Gleasonian manner... resulting in range shifts with varying rates, at different times, and in divergent directions." This prediction, that species should have independent colonization histories, is based primarily on fossils classified to species (Graham et al. 1996) and contrasts with the repeated pattern of intraspecific diversification in the Pacific Northwest identified using molecular markers. We cannot address the rate or timing of movement of these taxa based on a single marker, however, these data suggest comparable colonization routes. Phylogeographic analysis of northwestern species of birds and mammals suggests that, within codistributed forest associated species (e.g., *M. americana*, Demboski et al. 1999;

Fig. 3. Distribution of the coastal and continental lineages of American pine marten (*M. americana*) (A) and northern flying squirrel (*G. sabrinus*) (B), and the distribution of closely related species of chickadees (*P. hudsonicus* and *P. rufescens*) (C) and warblers (*D. coronata* and *D. auduboni*) (D).



Glaucomys sabrinus, Arbogast 1998; *Parus hudsonicus* and *Parus rufescens*, Gill et al. 1993; *Dendroica coronata* and *Dendroica auduboni*, Bermingham et al. 1992; Fig. 3), taxa tend to overlap spatially (Clementsian manner), as opposed to exhibiting independent colonization (Gleasonian manner).

The presence of multiple lineages within various species in southeast Alaska indicates that geography and evolution have profoundly affected community assembly. Even though numerous examples (e.g., May 1990; Raven and Wilson 1992) point to the danger of attempting to manage wildlife without an understanding of geographic variation, these distinct lineages have not been acknowledged in resource-management plans for the region (MacDonald and Cook 1996). This recurrent theme of lineage diversification should be explored further, particularly given the potential impact of deforestation on biotic communities in the Pacific Northwest.

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